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Research Article

Differentiation in the ultrastructure of pectiniform antennae in species groups of the genus *Ctenoceratoda* Varga, 1992 (Lepidoptera, Noctuidae)

Zoltán Varga[1], László Ronkay[2], László Rákosy[3]

1 *Department of Evolutionary Zoology and Human Biology, University of Debrecen, H-4032 Debrecen, Egyetem tér 1, Hungary*

2 *Heterocera Ltd, H-1137 Budapest, Szent István krt 4, Hungary*

3 *Faculty of Biology and Geology, Babęs-Bolyai University, 44 Republicii, RO-400015 Cluj-Napoca, Romania*

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Corresponding author: Zoltán Varga (varga.zoltan@science.unideb.hu)

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Abstract

We studied the types of sensilla on the pectinated antennae of *Ctenoceratoda* species (Noctuinae, Hadenini) using scanning electron microscopy. These ultrastructures are described, illustrated and analysed in four distinct species groups of the genus. The group features distinguishing the four lineages of the genus and their taxonomic importance are discussed.

Key Words

Poliina, reproductive isolation, scanning electron microscopy, sensilla chaetica, sensilla coeloconica, sensilla trichoidea, sister species, species groups

Introduction

Antennae belong to the most important developments of the cephalisation of Arthropods, incl. insects. They have a fundamental role in orientation, feeding and reproductive behaviour of the individuals. Most numerous sensory organs are concentrated on the head and on the antennae. The antennae are supplied by an abundance of sensory structures (sensilla). They function as the transmitting interface between the environment and the nervous system of the insect. The specialized receptor cells in these sensilla are fitted to detect the surroundings and transmit the information to the central nervous system that make decisions on behaviours such as host and mate selection, recognition, discrimination and acceptance vs refusing for mating or feeding (Shields and Hildebrand 2001). They appear mostly as different forms of bristles, hairs, pegs or cones, with different physical (mechano-, thermo- or hygroreceptors) and/or chemical (olfactory and gustatory) functions. These structures were originally described, depicted and typified based on light microscopic studies (Keil 1999; Stange and Stowe 1999), and more recently, using scanning (SEM) and/or transmission electron microscopy (TEM) (e.g. Drilling and Klass 2010; Sun et al. 2011; Galvania et al. 2012; Diongue et al. 2013; Zheng et al. 2014; Zhou et al. 2015; Thammaiah et al. 2021).

Numerous morphological studies on antennal and proboscis sensilla are mostly concerned with economically important taxa of Pyralidae (Castrejón Gómez et al. 2003; Sun et al. 2011), Gelechiidae (Bawin et al. 2017), Tortricidae (Roh et al. 2016, 2018), Hesperiidae (Yuan et al. 2014), Saturniidae (da Silva et al. 2019), Erebidae (Zheng et al. 2014; Santos et al. 2019), Noctuidae (Castrejón-Gómez et al. 1999; Diongue et al. 2013; Xue and Hua 2014; Chang et al. 2015; Seada 2015; Xue et al. 2016; Thammaiah et al. 2021), and they are focused on acceptance of sexual pheromones and/or chemical cues of food sources.

We surveyed the noctuid genus *Ctenoceratoda* Varga, 1992 (Noctuinae, Hadenini, Poliina) consisting of numerous

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species groups and pairs of sibling species, which can be often hardly identified by traditional morphological methods. This genus was separated from the most closely related genera of the subtribe Poliina by the conspicuous external habitus and the extremely elongate, bipectinate antennae of males (Varga 1992; Varga and Gyulai 1999; Varga et al. 2018). The species of the genus are also characterised by the somewhat simplified, completely symmetrical genital capsule combined with sophisticated lock-and-key structures of the inner genitalia. Thus, the male genitalia of *Ctenoceratoda* species are often rather weakly differentiated, however, the pectination of antennae seems to be more clearly distinct in different species and species groups.

Therefore, we hypothesised that the differentiation of the antennae may be responsible for the reproductive isolation of the externally and structurally weakly differentiated sister species. Thus, we surveyed the microscopic structures of the "pectination" of the male antennae in different magnifications, using scanning electron microscopy.

Material and methods

We followed in this survey the nomenclature of the antennal structures introduced by Keil (1999), applied for Noctuidae by Calatayud et al. (2006) and modified by Chang et al. (2015). Since the antennae are principally bilaterally symmetrical, we usually separated the right-sided antennae of the specimens. Since most species of *Ctenoceratoda* are represented in different museum collections by very limited material, we generally truncated only one or two male specimens of each species. Altogether, we had the opportunity to investigate 21 specimens of 13 different taxa. Therefore, we did not intend to make any statistical comparisons between the related species.

Ultrastructural analysis was performed using a Scanning electron microscope/SEM Jeol JSM 5510LV in high vacuum mode in the Scanning Electron Microscope Laboratory of the Dept. Taxonomy and Ecology of the University Babeş-Bolyai (Cluj-Napoca). Sample preparation: The carefully dried and dust-controlled antennae were mounted on aluminium stubs using one-sided adhesive tape, and the samples were covered with gold in three cycle depositions, each with a thickness of 4 nm, with an Agar Auto-Sputter-Coater. Then, the samples were examined and photographed in at least six different magnifications from 15× to 5500×. The magnifications 60×, 100× and 300× proved generally the most suitable for comparisons among the different species and species groups. On the photoplates some figures are vertically turned for better comparisons.

Characterisation of the target species groups

In the last revision of the subtribe Poliina (Varga et al. 2018), the genus *Ctenoceratoda* was subdivided into seven species groups. From these, we selected specimens from the following four species groups for our survey (*Paratype specimens were studied).

(i) The *Ctenoceratoda sukharevae* species group: the species pair *C. sukharevae* (Varga, 1974) – *C. oxyptera* Varga, 1992*. *C. sukharevae* was designated as type species of the genus (Varga 1992). There are some further species of this group which are only represented by a few specimens in the collections (*C. juliannae* Varga, 1992, *C. longicornis* (Graeser, 1892), *C. lukhtanovi* Varga & Gyulai, 1999, *C. stenocera* Varga & Gyulai, 2002). These have – with the exception of *C. juliannae*, sister species of *C. sukharevae* – shorter pectinated antennae than *C. sukharevae* and its closely related species *C. oxyptera*.

(ii) The *Ctenoceratoda khorgossi* species group. This group consists of five species, however, specimens were only available from three species, i.e. *C. khorgossi* (Alphéraky, 1882), *C. persephone* Varga, Gyulai, G. Ronkay & L. Ronkay, 2018* and *C. argyrea* Varga, 1992*. *C. khorgossi* and *C. persephone* are allopatric sister species, *C. argyrea* is sympatric with, but seems to be phenologically differentiated from *C. persephone*.

(iii) The *Ctenoceratoda tancrei* species group. The members of the species pair *C. tancrei* (Graeser, 1892) – *C. graeseri* (Püngeler, 1898) are partially sympatric but occur in different habitat types. *C. tancrei* inhabits dry rupicolous swards in Kazakhstan and Kirghizia in medium or high altitudes, while *C. graeseri* is connected to lowland sandy dune areas with halophilous scrubby vegetation.

(iv) The *Ctenoceratoda contempta* (Püngeler, 1914) species group: Two pairs of allopatric sister taxa were surveyed: *C. contempta* from Kirghizia (Naryn, near to the type locality) – *C. septemlacustris* Gaal-Haszler, Lödl, Ronkay, Ronkay & Varga, 2012* from NE Afghanistan (Wakhan), and *C. mallopyga mallopyga* Varga, Gyulai, G. Ronkay & L. Ronkay, 2018* (Pakistan, Karakoram) – *C. mallopyga dyschroa* Varga, Gyulai, G. Ronkay & L. Ronkay, 2018* (India, Himalaya). All these species occur in high altitude semi-desert regions.

Results

General characterisation of the sensilla

The long bipectinate antennae of *Ctenoceratoda* species are densely covered by sensilla (Fig. 1A). We generally distinguished three different types of sensilla (following the terminology of Calatayud et al. 2006). The sensilla chaetica (sing.: sensillum chaeticum, syn.: setae chaeticae, see: Chang et al. 2015) are about 100–150 µm long, they are loosely scattered on the stalk and on the dorsal side of the pectiniform processes of antennae. One single or some few (2–3) strong sensilla are obligatorily positioned on the

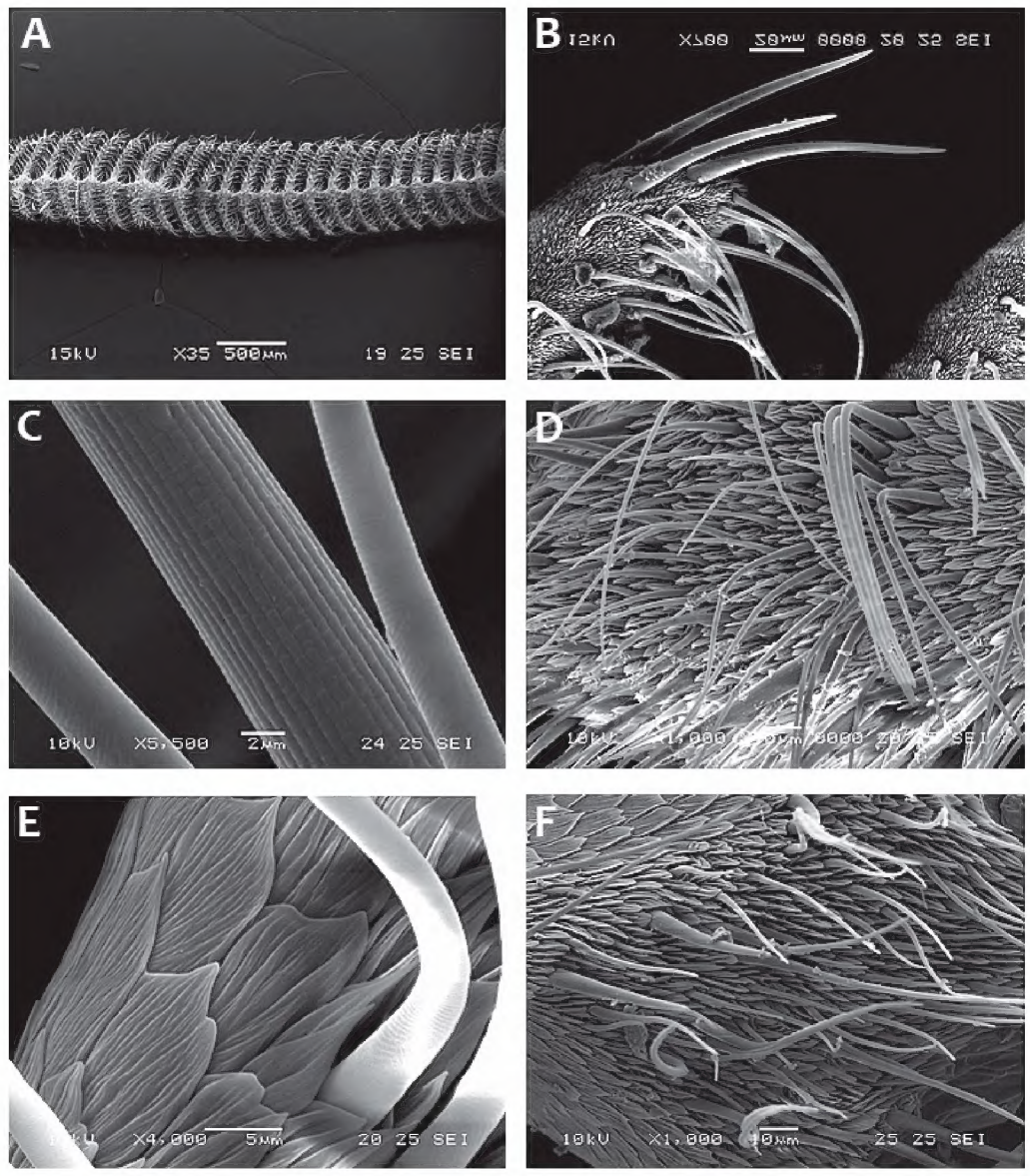

Figure 1. A. *C. sukharevae* (Varga, 1974), antenna general view, 35× magnification; **B.** *C. khorgossi* (Alpheraky, 1882), sensilla chaetica in terminal and subterminal position, sensilla trichoidea in subterminal and lateral position on a dorsal extension, 700× magnification; **C.** *C. peregovitsi* Varga & Gyulai, 1999, surface of sensillum chaeticum with longitudinal grooves and smooth surface of sensilla trichoidea, 5500× magnification; **D.** *C. mallopyga dyschroa* Varga, Gyulai, G. Ronkay & L. Ronkay, 2017, medially and terminally curved sensilla trichoidea, densely settled acute sensilla coeloconica on the stalk, 1000× magnification; **E.** *C. tancrei* (Graeser, 1892), ivy-leaf shaped sensilla coeloconica on a dorsal extension, 4000× magnification; **F.** *C. turpis* (Staudinger, 1900), ivy-leaf shaped and narrow, acute sensilla coeloconica on the stalk of the antenna, 1000× magnification.

tip of the processes (Fig. 1B). These sensilla bear numerous shallow longitudinal grooves on the surface (Fig. 1C).

The pectiniform processes and the stalk of the antennae are usually densely covered by the much thinner sensilla trichoidea. These are much finer, tapering terminally and do not show any surface patterns. They appear at least in two different forms: these are either straight or curved bristles or have a "flagellate" terminal part (Fig. 1D). The proportion of these types seems to be different in the species groups and species (details below).

The sensilla coeloconica (syn: setae coeloconicae) are generally leaf-shaped, either broader, remembering on ivy-leaves or much thinner and acute (Fig. 1E, F). These scales densely cover the surfaces of the stalk and the processes forming a cone-like structure. The shape of these sensilla seem to be highly variable, even on different parts of the antennae, they have, however, certain taxonomical significance (see below).

Comparison of the species groups, characterisation of the processes of antennae

The general structure of the antennae is rather uniform in the entire genus (see: diagnosis) with the exception of the taxonomically isolated species *C. zetina* (Staudinger, 1900). The pectiniform processes are extremely long and thin in the *C. khorgossi* group, oppositely, they are relatively short and thick in the *C. contempta* group. We accidentally observed also malformed, fused segments, most extremely in *C. oxyptera* (see: Discussion).

The *Sukharevae*-group. We studied only two species from the six known members of this species group. In *C. sukharevae*, the dorsal vs ventral pectiniform processes are supplied with some strong, nearly equally long sensilla chaetica in terminal and termino-lateral position, and with very numerous long, apically flagellate sensilla trichoidea, as well. The sensilla trichoidea are arranged in verticilia-like groups along the axis of the processes but irregularly scattered on the stalk of the antenna. Both the stalk and the processes are densely covered with apically acute ivy-leaf-shaped sensilla coeloconica (Fig. 2A–F).

The structures of the two closely related species are generally similar, with some specific differences, however. The pectiniform processes of *C. oxyptera* are more asymmetrical and the ventral extensions are curved terminally. The processes are usually bearing only a single sensillum chaeticum in terminal position, the sensilla trichoidea are somewhat thicker, curved terminally, more scarcely dispersed. The acute ivy-leaf-shaped sensilla coeloconica are essentially narrower (Fig. 3A–F).

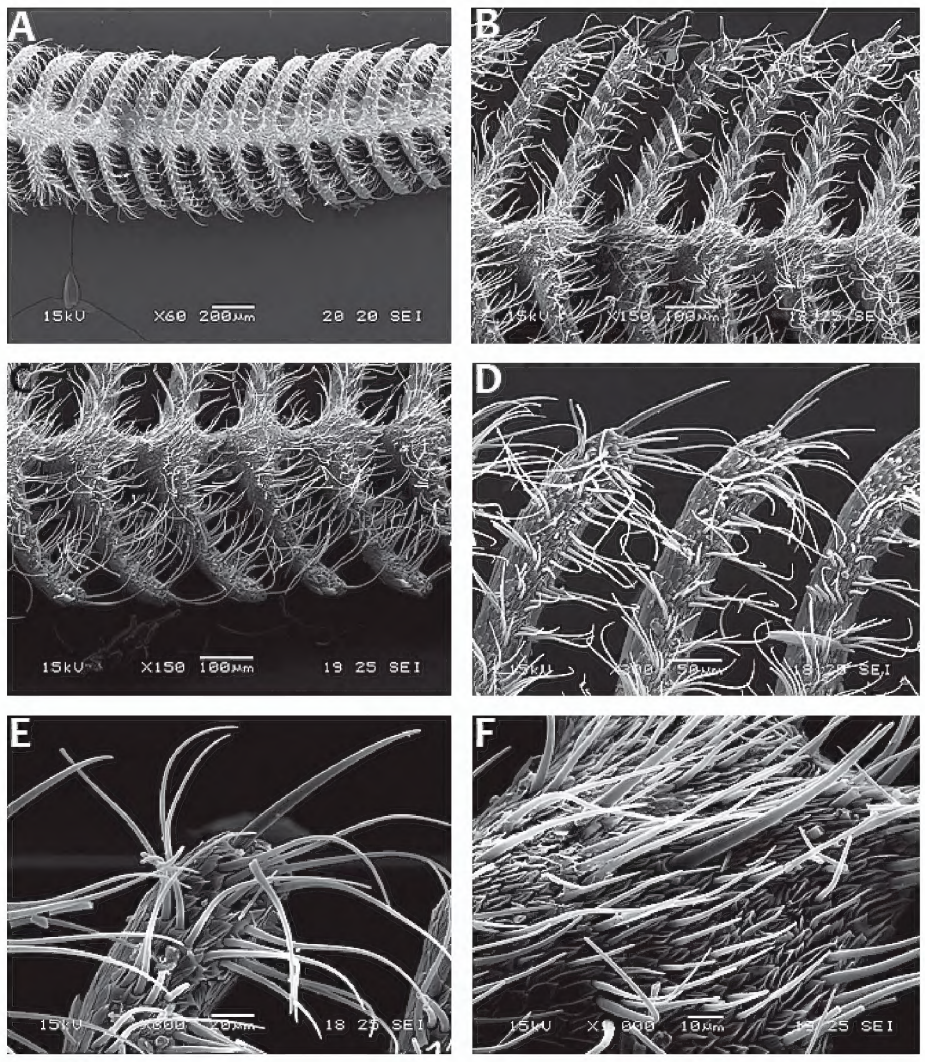

Figure 2. A. *C. sukharevae* (Varga, 1974), medial part of the antenna, with bilateral processes, 60× magnification; **B.** *C. sukharevae* (Varga, 1974), dorsal processes of the antenna with straight sensilla chaetica in terminal and subterminal position, and sensilla trichoidea arranged in loose verticils, the extension and stalk are densely covered with sensilla coeloconica, 150× magnification; **C.** *C. sukharevae* (Varga, 1974), ventral processes of the antenna with curved sensilla chaetica, and medially or terminally curved sensilla trichoidea, 150× magnification; **D.** *C. sukharevae* (Varga, 1974), terminal part of the dorsal process with straight sensilla chaetica and numerous sensilla trichoidea, 300× magnification; **E.** *C. sukharevae* (Varga, 1974), tip of a dorsal process, the sensillum chaeticum is striated longitudinally, the sensilla trichoidea are smooth and slightly curved, 600× magnification; **F.** *C. sukharevae* (Varga, 1974), different types of sensilla on the stalk, densely covered by narrow sensilla coeloconica, 1000× magnification.

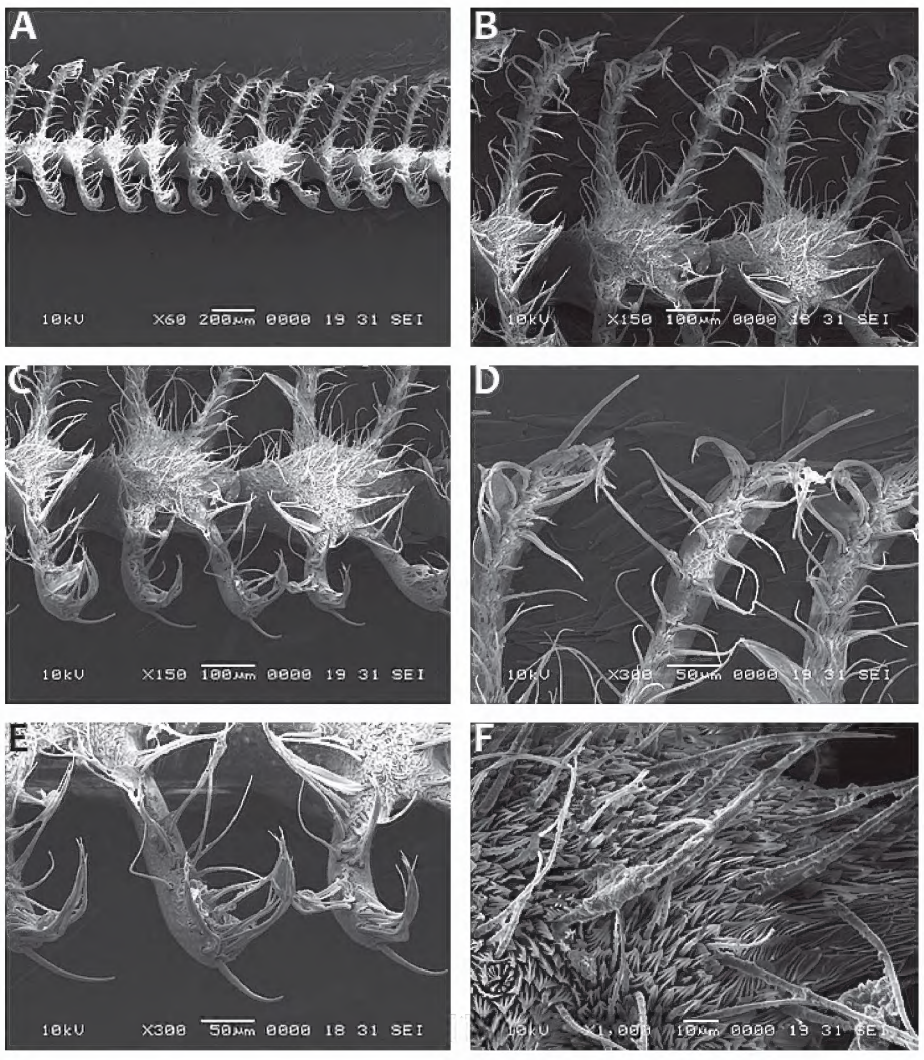

Figure 3. A. *C. oxyptera* Varga, 1992, medial part of the antenna, with bilateral processes, some segments are teratologically fused, 60× magnification; **B.** *C. oxyptera* Varga, 1992, dorsal processes on the medial part of the antenna with sensilla chaetica in terminal position and scarce, rough sensilla trichoidea, two × two segments are teratologically fused, 150× magnification; **C.** *C. oxyptera* Varga, 1992, teratologically fused segments, ventral processes with curved sensilla chaetica in terminal position, and curved, loosely dispersed sensilla trichoidea, 150× magnification; **D.** *C. oxyptera* Varga, 1992, terminal part of the dorsal processes with slightly curved sensilla chaetica, striated longitudinally, and with scarce, rough sensilla trichoidea, 300× magnification; **E.** *C. oxyptera* Varga, 1992, ventral processes with curved sensilla chaetica, with curved, rough and finer sensilla trichoidea, 300× magnification; **F.** *C. oxyptera* Varga, 1992, part of the stalk with different sensilla, densely covered by sensilla coeloconica, 1000× magnification.

The *Khorgossi*-group. The bilateral processes of the pectinated antennae are long, thin and clearly asymmetrical, usually with a single strong sensillum chaeticum in terminal position. The sensilla trichoidea are thin, are shorter than in the *sukharevae*-group and not flagellate, they are more scattered and not arranged in verticilia. The sensilla coeloconica are narrow and acute, very densely covering the surface of the processes. The details of the structures of the allopatric sister species *C. khorgossi* (Fig. 4A–F) and *C. persephone* (Fig. 5A–F) are essentially identical but some traits are more extremely expressed in *C. persephone*. In the latter species, the sensilla trichoidea are on average much longer than in *C. khorgossi* and often also slightly flagellate, especially those which are in subterminal position. *C. argyrea* (Fig. 6A–F) is more differentiated in all features than the former two sister species from each other. The terminal sensilla chaetica are relatively shorter, the sensilla trichoidea are stronger, more bristle-shaped than in the *khorgossi-persephone* species pair. The sensilla coeloconica are also broader, more ivy-leaf-shaped.

The *Tancrei*-group. This species group displays a peculiar combination of the characters of the former two species groups. The bilateral processes of the pectinated antennae are of medium length and nearly symmetrical. The sensilla chaetica in terminal position are slightly curved and relatively short, essentially shorter than the average length of the sensilla trichoidea. The sensilla trichoidea are strong, medially curved, and they are arranged in loose verticils on the processes, while the sensilla coeloconica are broad and ivy-leaf-shaped. The two species of this group are, in correspondence with their sister species status, only slightly differentiated from each other. In *C. graeseri* (Figs 7A–F, 8A, B), the terminal sensilla chaetica are somewhat longer and stronger patterned longitudinally than in *C. tancrei* (Figs 9A–F, 10A–F).

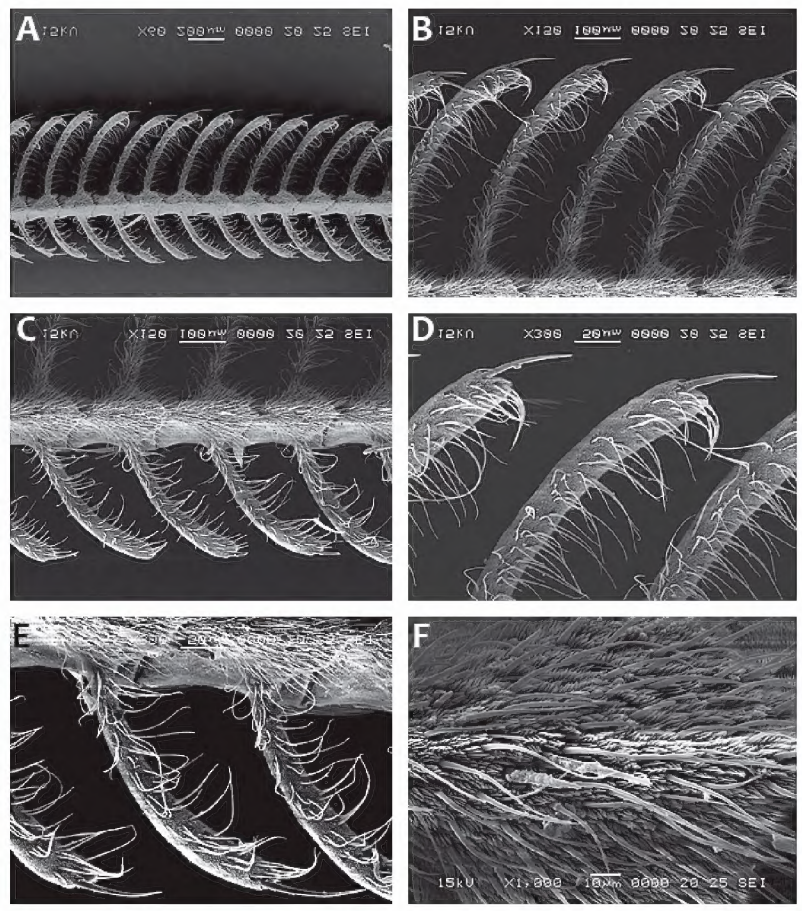

Figure 4. A. *C. khorgossi* (Alpheraky, 1882), medial part of the antenna, with thin and asymmetrical bilateral processes, with strong sensilla chaetica in terminal position, and numerous fine, long sensilla trichoidea, 60× magnification; **B.** *C. khorgossi* (Alpheraky, 1882), elongate dorsal processes with strong sensilla chaetica in terminal position, and numerous fine, long sensilla trichoidea, being curved in subterminal position, 150× magnification; **C.** *C. khorgossi* (Alpheraky, 1882), shorter ventral processes with shorter sensilla chaetica in terminal position, and numerous fine, long sensilla trichoidea, 150× magnification; **D.** *C. khorgossi* (Alpheraky, 1882), terminal part of the dorsal processes with strong sensilla chaetica, striated longitudinally, and with long, thin sensilla trichoidea, 300× magnification; **E.** *C. khorgossi* (Alpheraky, 1882), ventral processes with strong, curved sensilla chaetica, with long and fine sensilla trichoidea, 300× magnification; **F.** *C. khorgossi* (Alpheraky, 1882), part of the stalk with different sensilla, densely covered by narrow, acute sensilla coeloconica, 1000× magnification.

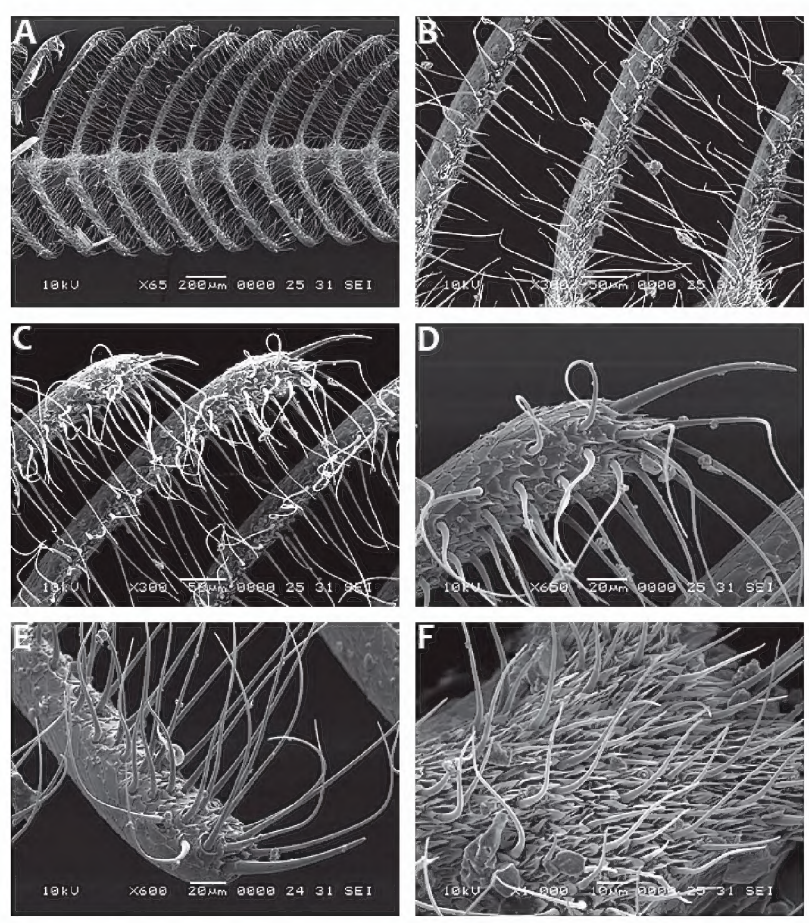

Figure 5. A. *C. persephone* Varga, Gyulai, G. Ronkay & L. Ronkay, 2017, medial part of the antenna, with very long and slightly asymmetric bilateral processes, with strong sensilla chaetica in terminal position, and numerous thin, very long sensilla trichoidea, 60× magnification; **B.** *C. persephone* Varga, Gyulai, G. Ronkay & L. Ronkay, 2017, medial part of the dorsal processes with very thin sensilla trichoidea, 300× magnification; **C.** *C. persephone* Varga, Gyulai, G. Ronkay & L. Ronkay, 2017, distal part of the dorsal processes with strong sensilla chaetica in terminal position and with stronger and very thin sensilla trichoidea, 300× magnification; **D.** *C. persephone* Varga, Gyulai, G. Ronkay & L. Ronkay, 2017, tip of a dorsal process with a strong sensilla chaetica, striated longitudinally, and with thin, partly flagellate sensilla trichoidea, 600× magnification; **E.** *C. persephone* Varga, Gyulai, G. Ronkay & L. Ronkay, 2017, tip of a ventral process with a strong sensillum chaeticum, striated longitudinally, and with thin, partly flagellate sensilla trichoidea, 600× magnification; **F.** *C. persephone* Varga, Gyulai, G. Ronkay & L. Ronkay, 2017, part of the stalk with various forms of sensilla trichoidea, densely covered by narrow, acute sensilla coeloconica, 1000× magnification.

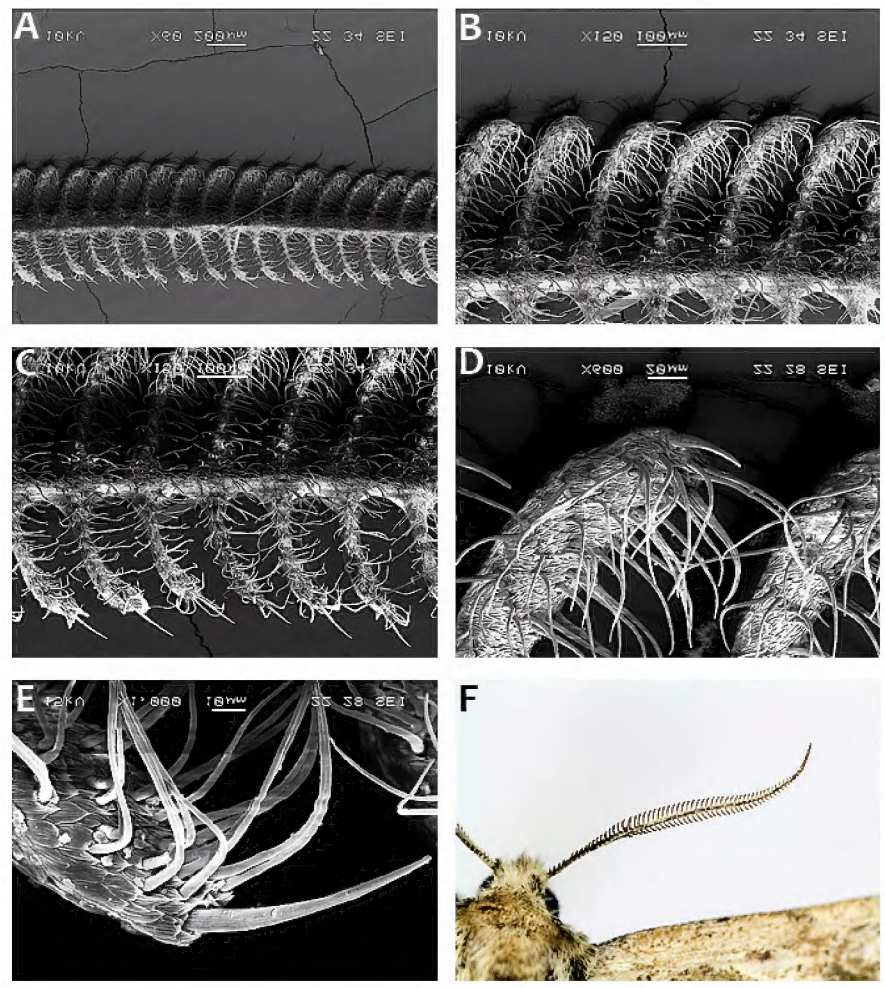

Figure 6. A. *C. argyrea* Varga, 1992, medial part of the antenna, with nearly symmetrical bilateral processes, with relatively short, curved sensilla chaetica in terminal position, and numerous sensilla trichoidea, 60× magnification; **B.** *C. argyrea* Varga, 1992, stalk and dorsal processes with short, curved sensilla chaetica and thin sensilla trichoidea, 150× magnification; **C.** *C. argyrea* Varga, 1992, stalk and ventral processes with strong sensilla chaetica in terminal position, and with numerous thin, curved or flagellate sensilla trichoidea, 150× magnification; **D.** *C. argyrea* Varga, 1992, distal part of a dorsal process with a relatively short sensillum chaeticum in terminal position, with thin and strong sensilla trichoidea, 600× magnification; **E.** *C. argyrea* Varga, 1992, distal part of a ventral process with a strong sensilla chaetica in terminal position and with medially curved strong sensilla trichoidea, 1000× magnification; **F.** *C. argyrea* Varga, 1992, general view of the head and antennae of the Paratype specimen.

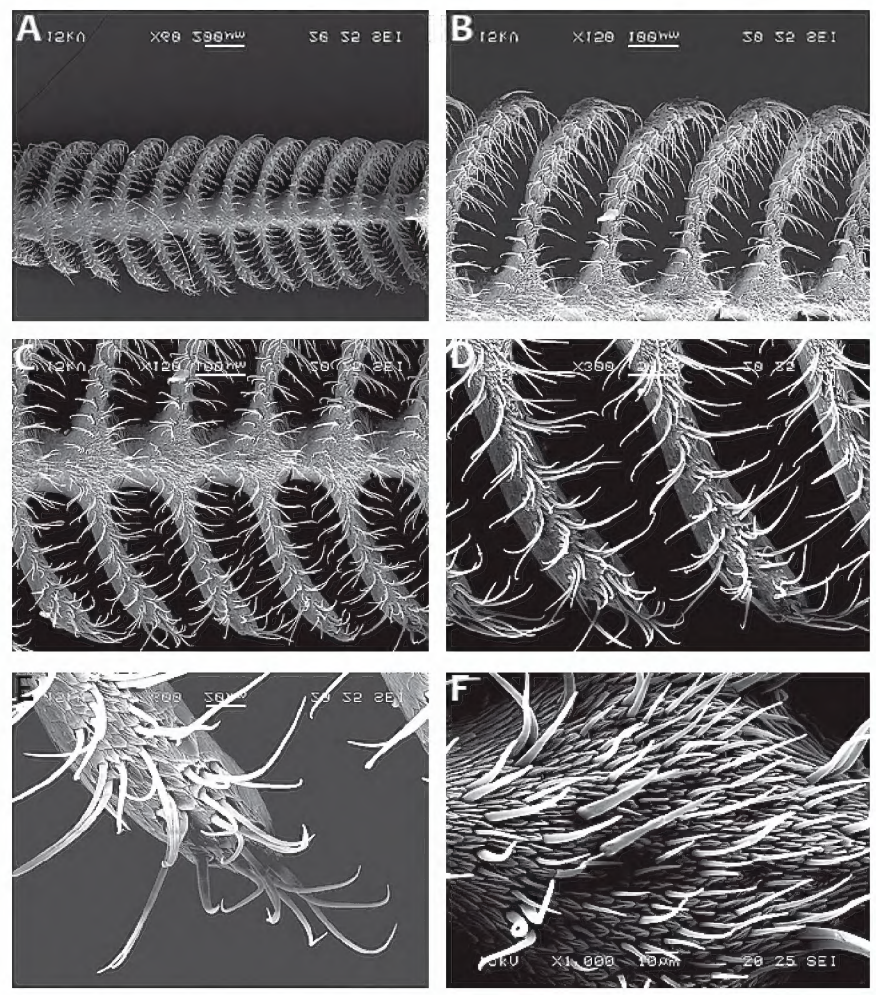

Figure 7. A. *C. tancrei* (Graeser, 1892), medial part of the antenna, with nearly symmetrical bilateral processes, with curved sensilla chaetica in terminal position, and numerous thin, declining sensilla trichoidea, 60× magnification; **B.** *C. tancrei* (Graeser, 1892), stalk and dorsal processes with curved sensilla chaetica and thin, long, curved sensilla trichoidea, arranged in loose verticils, 150× magnification; **C.** *C. tancrei* (Graeser, 1892), stalk and ventral processes with relatively short sensilla chaetica in terminal position, and with thin, curved sensilla trichoidea, 150× magnification; **D.** *C. tancrei* (Graeser, 1892), distal part of the ventral processes with relatively short and weak sensilla chaetica in terminal and subterminal position, and with curved or flagellate sensilla trichoidea, 300× magnification; **E.** *C. tancrei* (Graeser, 1892), terminal part of a ventral process with weak, curved sensilla chaetica and with slightly curved sensilla trichoidea, 600× magnification; **F.** *C. tancrei* (Graeser, 1892), part of the stalk with sensilla trichoidea, densely covered by narrow, acute sensilla coeloconica, 1000× magnification.

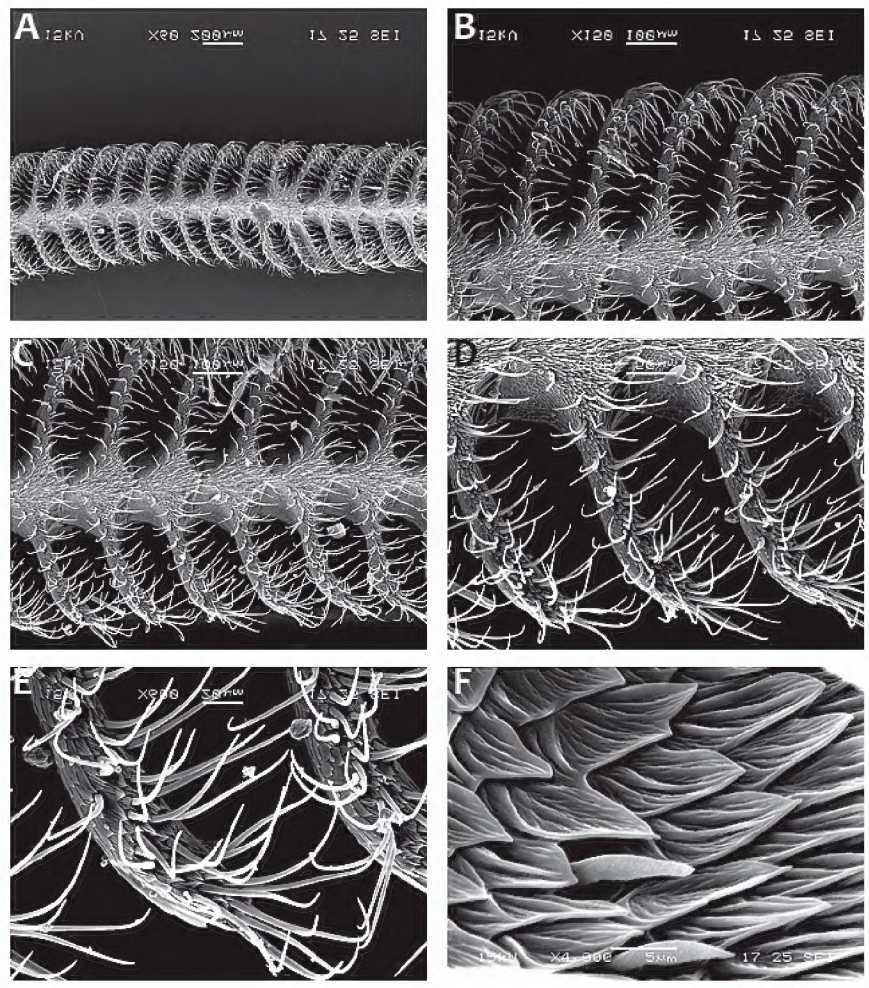

Figure 8. A. *C. tancrei* (Graeser, 1892), medial part of the antenna, with some malformed segments and nearly symmetric bilateral processes, with curved sensilla chaetica in terminal position, and numerous thin, slightly curved and declining sensilla trichoidea, 60× magnification; **B.** *C. tancrei* (Graeser, 1892), stalk and dorsal processes with curved sensilla chaetica and curved thin sensilla trichoidea, arranged in loose verticils, 150× magnification; **C.** *C. tancrei* (Graeser, 1892), stalk and ventral processes with short sensilla chaetica and curved or flagellate sensilla trichoidea, arranged in verticils, 150× magnification; **D.** *C. tancrei* (Graeser, 1892), ventral processes with curved sensilla chaetica and numerous curved or flagellate sensilla trichoidea, 430× magnification; **E.** *C. tancrei* (Graeser, 1892), distal part of a ventral process with straight sensilla chaetica and flagellate sensilla trichoidea, 600× magnification; **F.** *C. tancrei* (Graeser, 1892), part of the stalk with sensilla trichoidea, densely covered by ivy-leaf shaped sensilla coeloconica, 4000× magnification.

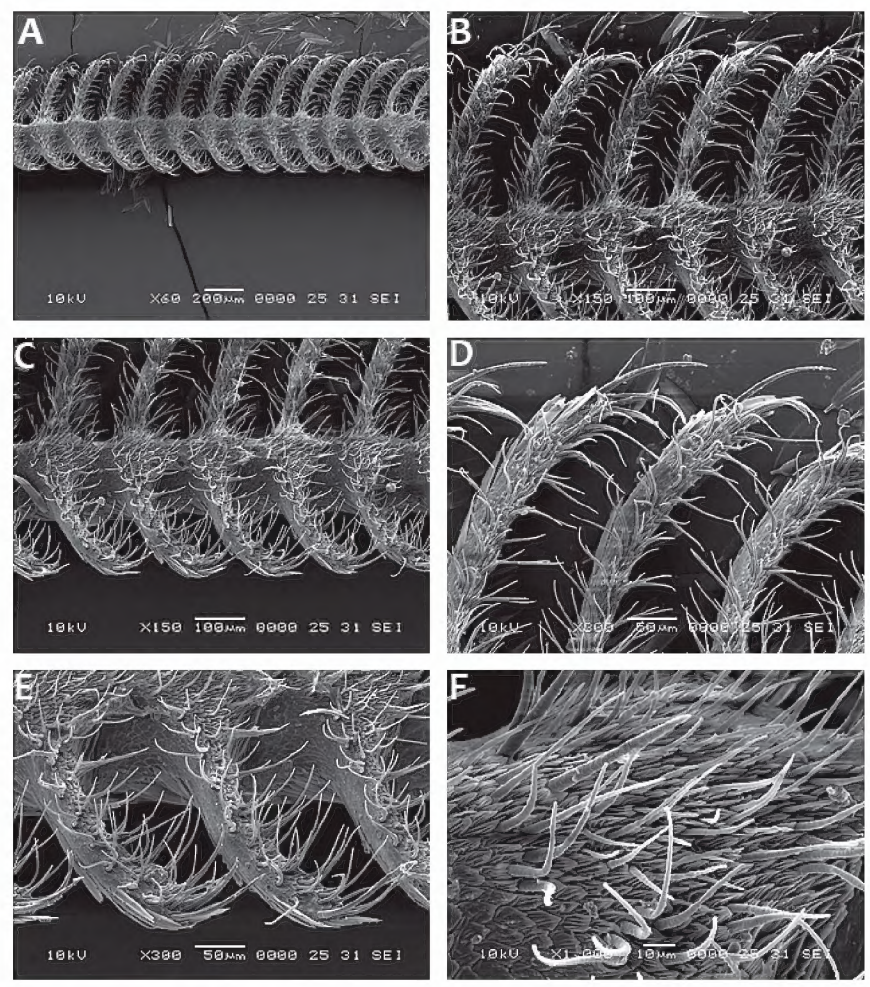

Figure 9. A. *C. graeseri* (Püngeler, 1898), medial part of the antenna, with slightly asymmetrical processes, with long sensilla chaetica in terminal position, and medially curved sensilla trichoidea, 60× magnification; **B.** *C. graeseri* (Püngeler, 1898), stalk and dorsal processes with long, straight or slightly curved sensilla chaetica and with straight or terminally curved sensilla trichoidea, 150× magnification; **C.** *C. graeseri* (Püngeler, 1898), stalk and ventral processes with strong, slightly curved sensilla chaetica and with straight or slightly curved sensilla trichoidea, 150× magnification; **D.** *C. graeseri* (Püngeler, 1898), distal part of dorsal processes with relatively short sensilla chaetica in terminal position and with straight or slightly curved sensilla trichoidea, 300× magnification; **E.** *C. graeseri* (Püngeler, 1898), ventral processes with relatively short sensilla chaetica in terminal position and with basally slightly curved sensilla trichoidea, 300× magnification; **F.** *C. graeseri* (Püngeler, 1898), part of the stalk with sensilla trichoidea, densely covered by narrow, acute sensilla coeloconica, 1000× magnification.

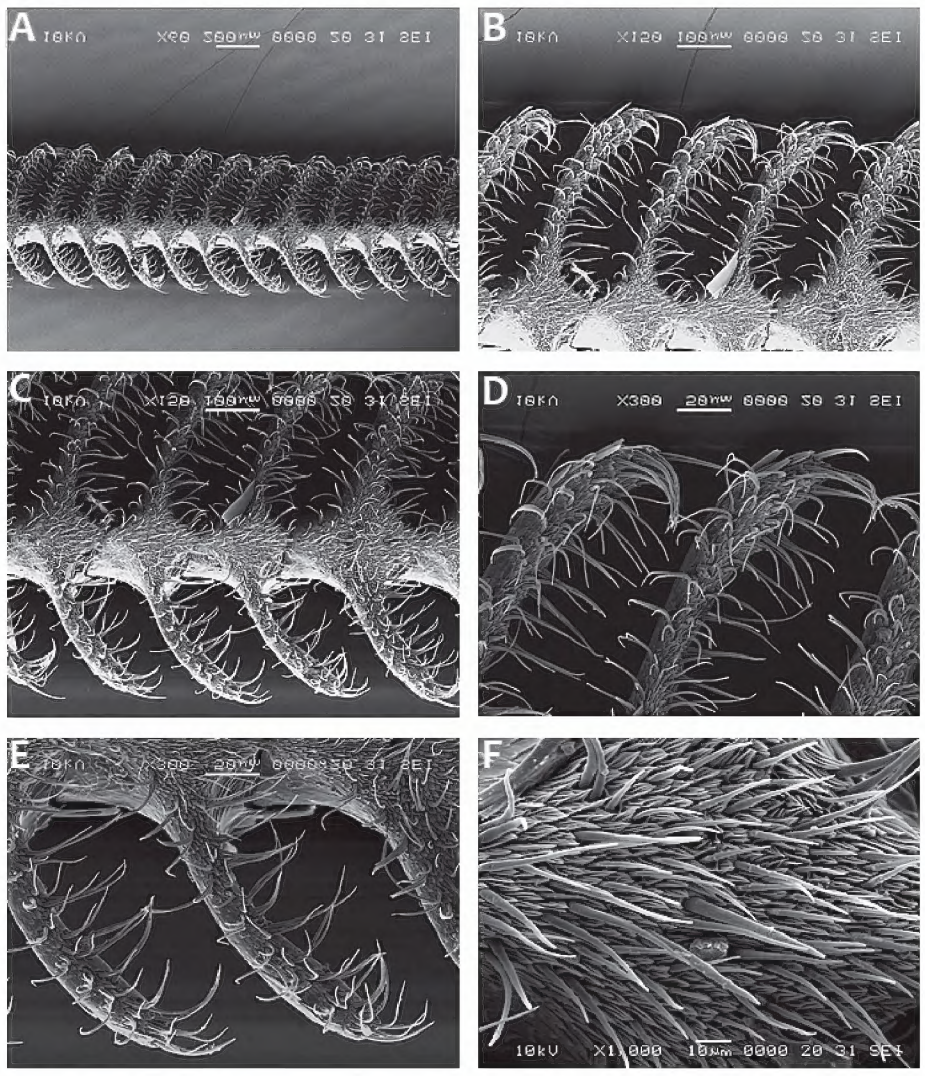

Figure 10. A. *C. graeseri* (Püngeler, 1898), medial part of the antenna, with asymmetrical processes, with long, slightly curved sensilla chaetica in terminal position, and scattered, medially curved sensilla trichoidea, 60× magnification; **B.** *C. graeseri* (Püngeler, 1898), stalk and dorsal processes with strong, curved sensilla chaetica in terminal position and with nearly straight sensilla trichoidea in verticils, 150× magnification; **C.** *C. graeseri* (Püngeler, 1898), stalk and ventral processes with strong, curved sensilla chaetica in terminal position and with slightly curved sensilla trichoidea in dense verticils, 150× magnification; **D.** *C. graeseri* (Püngeler, 1898), distal part of the dorsal processes with strong, curved sensilla chaetica in terminal position and with straight or basally curved sensilla trichoidea, 300× magnification; **E.** *C. graeseri* (Püngeler, 1898), ventral processes with strong sensilla chaetica in terminal position and with strong, nearly straight or curved sensilla trichoidea, 300× magnification; **F.** *C. graeseri* (Püngeler, 1898), part of the stalk with sensilla trichoidea, densely covered by narrow, acute sensilla coeloconica, 1000× magnification.

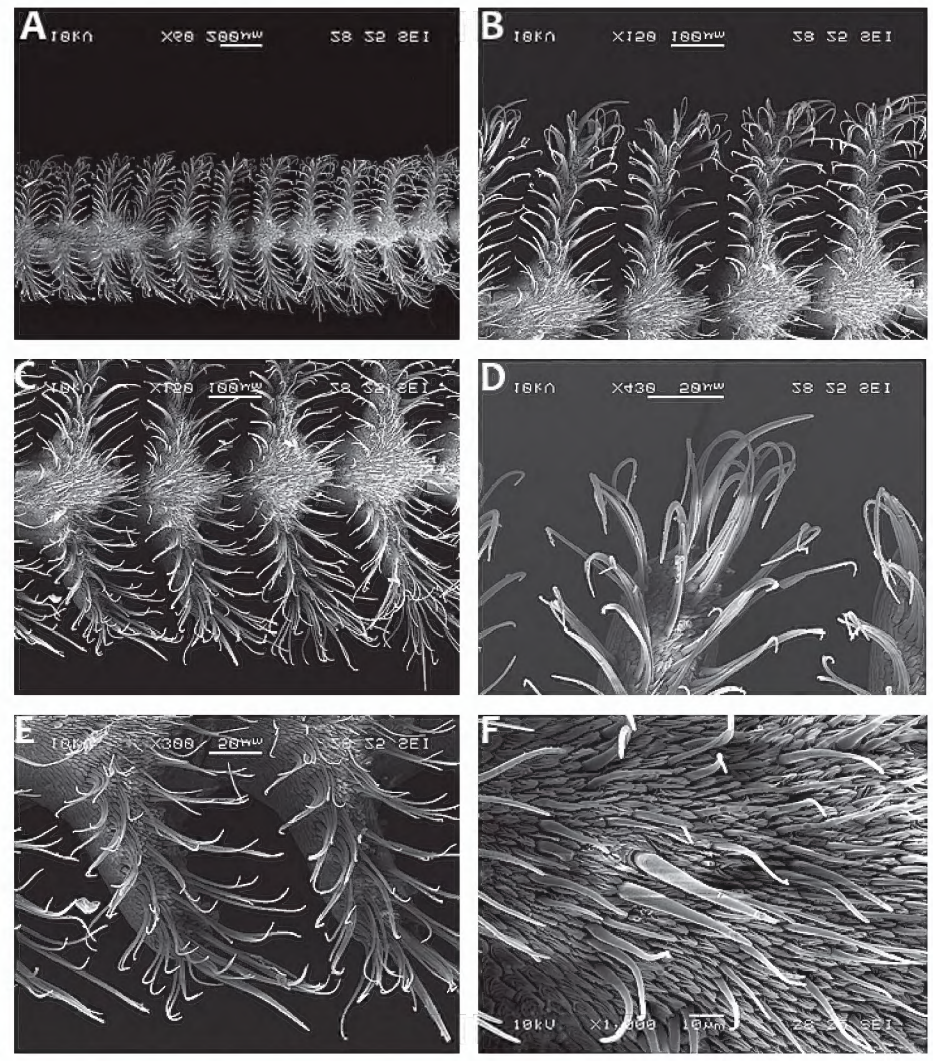

Figure 11. A. *C. contempta* (Püngeler, 1914) medial part of the antenna, with asymmetrical processes, with long, curved sensilla chaetica in terminal position, and with straight or terminally curved sensilla trichoidea, 60× magnification; **B.** *C. contempta* (Püngeler, 1914) stalk and dorsal processes of the antenna, with strong, claw-shaped sensilla chaetica in terminal position and with straight or terminally curved sensilla trichoidea, 150× magnification; **C.** *C. contempta* (Püngeler, 1914) stalk and ventral processes of the antenna with curved sensilla chaetica in terminal position and with straight or curved sensilla trichoidea, 150× magnification; **D.** *C. contempta* (Püngeler, 1914) distal part of the dorsal processes with strong claw-shaped sensilla chaetica in terminal and subterminal position and with strong or finer, straight or curved sensilla trichoidea, 300× magnification; **E.** *C. contempta* (Püngeler, 1914) ventral processes with somewhat shorter, curved sensilla chaetica and with strong or finer, curved sensilla trichoidea, 300c magnification; **F.** *C. contempta* (Püngeler, 1914) part of the stalk with sensilla trichoidea, densely covered by narrow, acute sensilla coeloconica, 1000× magnification.

The *Contempta* group. This species group is most differentiated from the other ones. The bilateral processes are slightly asymmetrical and essentially shorter than in the other species groups. The terminal sensilla chaetica are very strong, straight and patterned longitudinally. The sensilla trichoidea are strong, curved medially or terminally and are arranged in loosed verticilia along the processes. The sensilla coeloconica are narrow, acute and are densely covering the stalk and the processes. The species group consists of two pairs of taxa, both of which have been taxonomically considered as allopatric sister taxa (Varga et al. 2018). In the *contempta-septemlacustris* pair (Figs 11A–F and 12A–F), the dorsal versus ventral processes are only slightly asymmetrical (in *C. septemlacustris* somewhat more), and the terminal sensilla chaetica are slightly curved, the sensilla trichoidea are strongly curved medially, and the sensilla coeloconica are rather densely settled, narrow and acute. In the *mallopyga-dyschroa* pair (Figs 13A–F and 14A–F), the dorsal versus ventral extensions are more asymmetrical, the terminal sensilla chaetica are straighter and the sensilla trichoidea are straight or slightly curved terminally on the extensions and sometimes curved medially on the stalk only. The sensilla coeloconica are slightly more acute than in the former species group.

Nearly the same types of antennal sensilla were also found in certain members of the widespread and diverse Holarctic genus *Polia* Ochsenheimer, 1816, including its recently separated Sino-Himalayan subgenus *Metallopolia* Varga, G. Ronkay & L. Ronkay, 2018 (Fig. 15A–F). The phylogenetic systematic questions con-

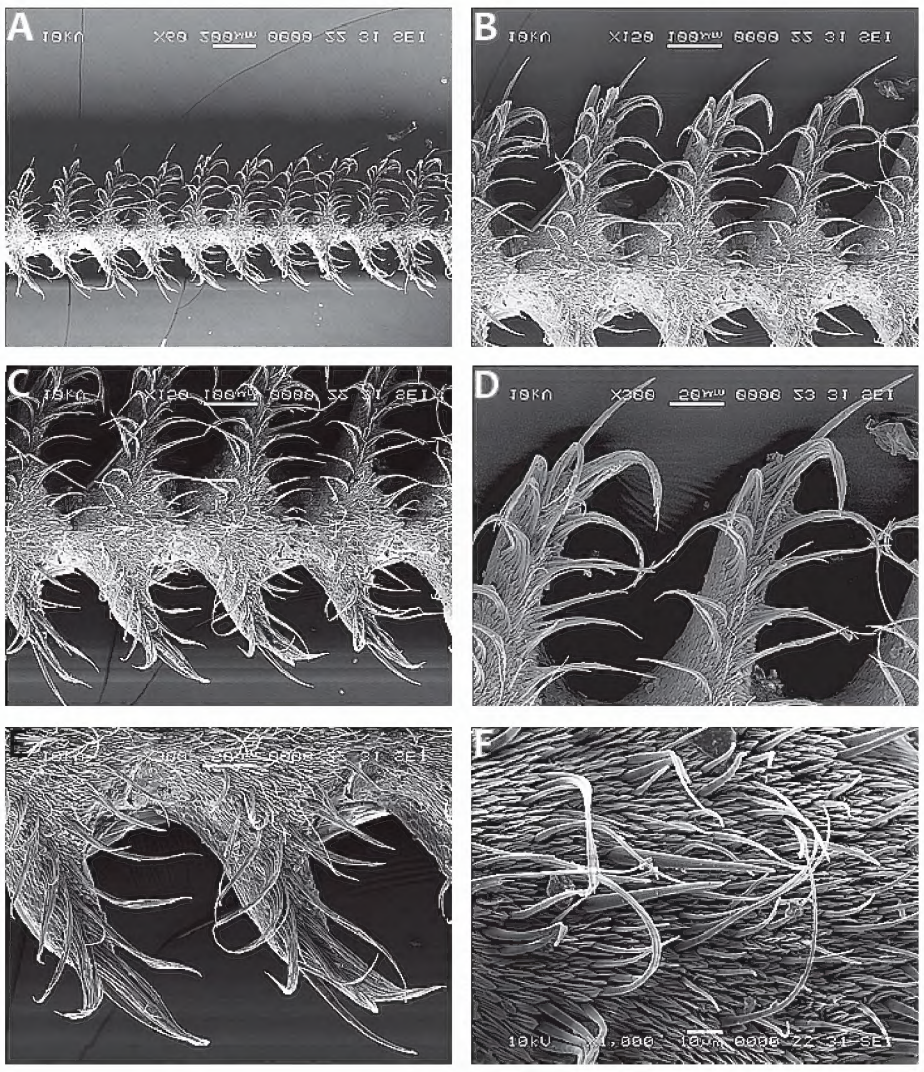

Figure 12. A. *C. septemlacustris* Gaal-Haszler, Lödl, Ronkay, Ronkay & Varga, 2012 medial part of the antenna, with somewhat shorter asymmetrical processes, with long, curved sensilla chaetica in terminal position, and with verticils of terminally curved, long sensilla trichoidea, 60× magnification; **B.** *C. septemlacustris* Gaal-Haszler, Lödl, Ronkay, Ronkay & Varga, 2012 stalk and dorsal processes of the antenna, with strong, curved sensilla chaetica in terminal position and with verticils of terminally curved sensilla trichoidea, 150× magnification; **C.** *C. septemlacustris* Gaal-Haszler, Lödl, Ronkay, Ronkay & Varga, 2012 stalk and ventral processes of the antenna, with nearly straight sensilla chaetica in terminal position and with verticils of terminally curved or flagellate sensilla trichoidea, 150× magnification; **D.** *C. septemlacustris* Gaal-Haszler, Lödl, Ronkay, Ronkay & Varga, 2012 terminal part of a dorsal process with a claw-shaped sensilla chaetica in terminal position and with verticils of terminally curved or recurved sensilla trichoidea, 300× magnification; **E.** *C. septemlacustris* Gaal-Haszler, Lödl, Ronkay, Ronkay & Varga, 2012 ventral processes of the antenna, with nearly straight sensilla chaetica in terminal position and with verticils of terminally curved or recurved sensilla trichoidea, 300× magnification; **F.** *C. septemlacustris* Gaal-Haszler, Lödl, Ronkay, Ronkay & Varga, 2012 part of the stalk with sensilla trichoidea, densely covered by narrow, acute sensilla coeloconica, 1000× magnification.

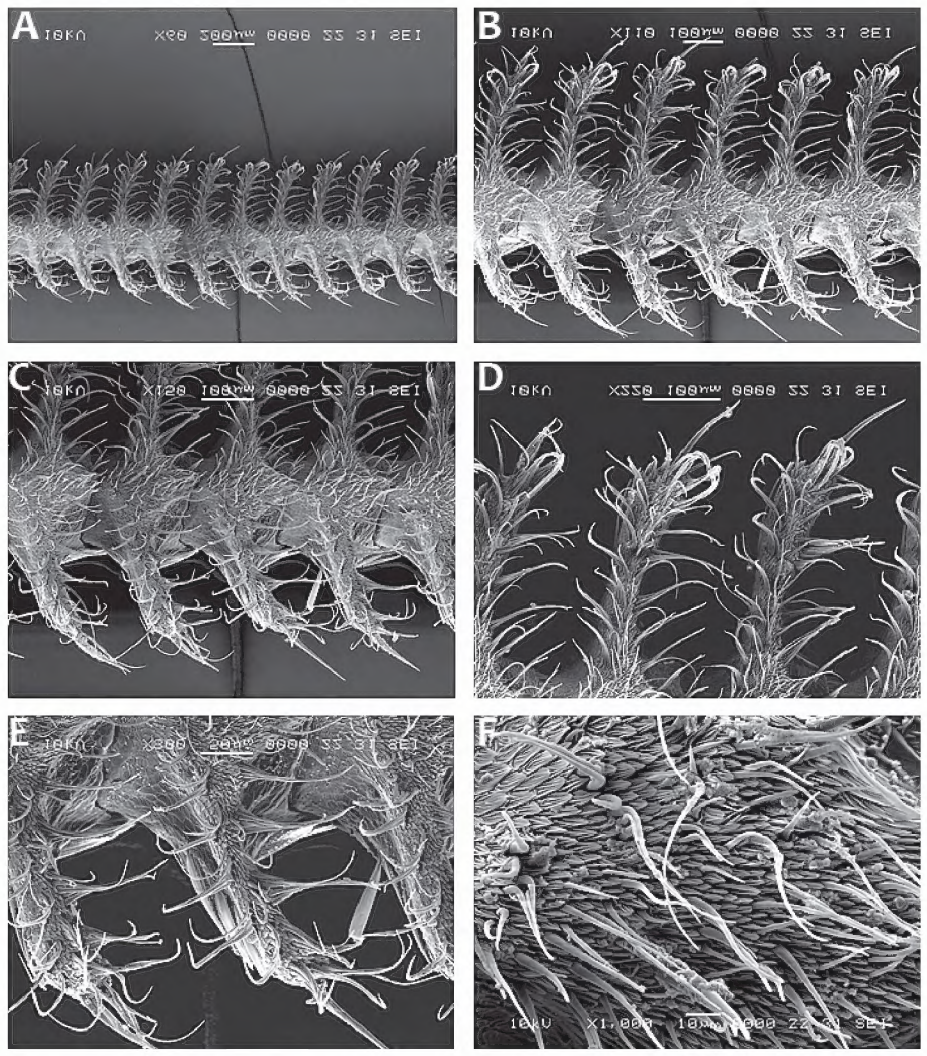

Figure 13. A. *C. mallopyga mallopyga* Varga, Gyulai, G. Ronkay & L. Ronkay, 2017, medial part of the antenna, with relatively short processes, with long sensilla chaetica in terminal position, and with medially or terminally curved sensilla trichoidea, 60× magnification; **B.** *C. mallopyga mallopyga* Varga, Gyulai, G. Ronkay & L. Ronkay, 2017, stalk and dorsal processes of the antenna, with long, nearly straight sensilla chaetica in terminal position, and with medially or terminally curved sensilla trichoidea, 150× magnification; **C.** *C. mallopyga mallopyga* Varga, Gyulai, G. Ronkay & L. Ronkay, 2017, stalk and the relatively short ventral processes of the antenna, with somewhat weaker sensilla chaetica in terminal position and with strong medially or terminally curved sensilla trichoidea, 150× magnification; **D.** *C. mallopyga mallopyga* Varga, Gyulai, G. Ronkay & L. Ronkay, 2017, distal part of the dorsal processes of the antenna, with long, nearly straight sensilla chaetica in terminal position, and with medially or terminally curved sensilla trichoidea,; **E.** *C. mallopyga mallopyga* Varga, Gyulai, G. Ronkay & L. Ronkay, 2017, short ventral processes of the antenna with sensilla chaetica in terminal position and curved sensilla trichoidea, 300× magnification; **F.** *C. mallopyga mallopyga* Varga, Gyulai, G. Ronkay & L. Ronkay, 2017, part of the stalk with relatively short and curved sensilla trichoidea, densely covered by narrow, acute sensilla coeloconica, 1000× magnification.

cerning these genera, representing a larger monophyletic clade of Hadenini (Varga et al. 2018), will be discussed in a forthcoming paper.

Discussion and taxonomic conclusions

Numerous earlier (e.g. Flower and Helson 1974; Liu and Liu 1984; Castrejón-Gómez et al. 1999) and more recent communications (Calatayud et al. 2006; Diongue et al. 2013; Chang et al. 2015; Xu et al. 2016; Thammaiah et al. 2021) concern the morphological and physiological types of antennal sensilla of Noctuid moths, mostly in economically important species (e.g. *Busseola fusca*, *Copitarsia consueta*, *Helicoverpa armigera*, *H. assulta*, *Mamestra configurata*, *Mythimna separata*), using the tools of scanning and transmission electron microscopy. The significance of these structures in the process of the speciation

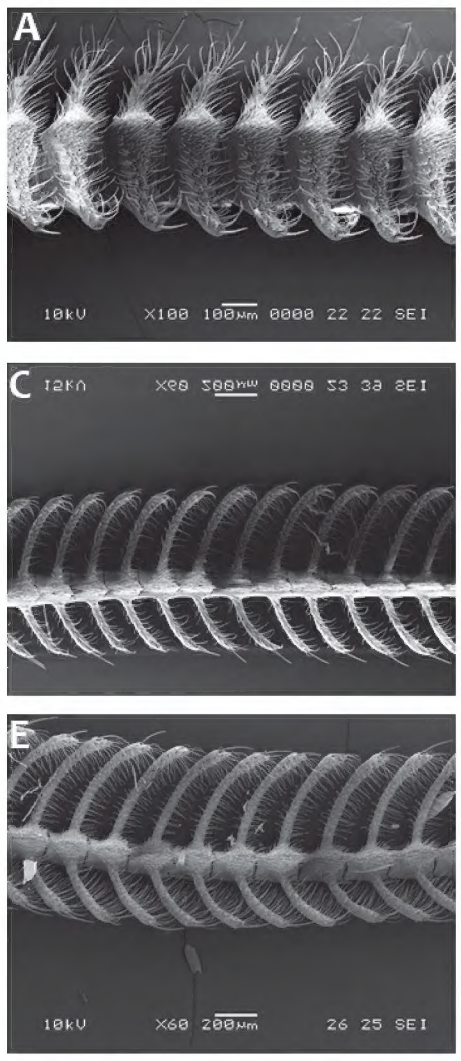

Figure 14. A. *C. mallopyga dyschroa* Varga, Gyulai, G. Ronkay and L. Ronkay, 2017, medial part of the antenna with short, asymmetric processes and with long sensilla chaetica in terminal position, with straight or terminally curved sensilla trichoidea, 60× magnification; **B.** *C. mallopyga dyschroa* Varga, Gyulai, G. Ronkay & L. Ronkay, 2017, stalk and dorsal processes of the antenna, with long, nearly straight sensilla chaetica in terminal position, and with straight or terminally curved sensilla trichoidea, 150× magnification; **C.** *C. mallopyga dyschroa* Varga, Gyulai, G. Ronkay & L. Ronkay, 2017, stalk and ventral processes of the antenna, with long, nearly straight sensilla chaetica in terminal position, and with straight or terminally curved sensilla trichoidea, 150× magnification; **D.** *C. mallopyga dyschroa* Varga, Gyulai, G. Ronkay & L. Ronkay, 2017, distal part of the dorsal processes with long, nearly straight sensilla chaetica in terminal position, and with nearly straight or terminally curved sensilla trichoidea, 300× magnification; **E.** *C. mallopyga dyschroa* Varga, Gyulai, G. Ronkay & L. Ronkay, 2017, short ventral processes of the antenna with straight sensilla chaetica in terminal position and terminally curved sensilla trichoidea, 300× magnification; **F.** *C. mallopyga dyschroa* Varga, Gyulai, G. Ronkay & L. Ronkay, 2017, part of the stalk with relatively short sensilla trichoidea, densely covered by narrow, acute sensilla coeloconica, 1000× magnification.

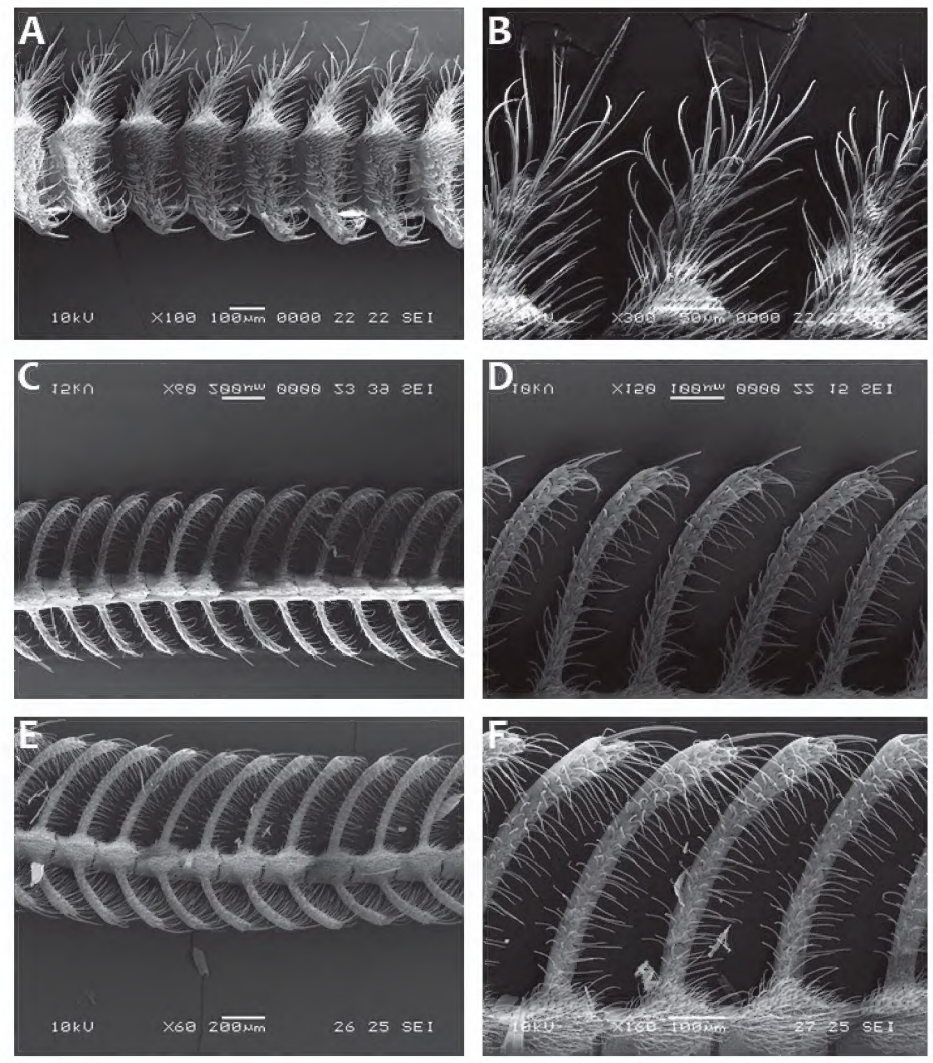

Figure 15. A. *Polia serratilinea* (Treitschke, 1825), medial part of the antenna with very short, slightly asymmetric processes, with long sensilla chaetica in terminal position, and with terminally curved sensilla trichoidea, 100× magnification.; **B.** *Polia serratilinea* (Treitschke, 1825), stalk and dorsal processes of the antenna, with strong, straight sensilla chaetica and densely situated terminally curved sensilla trichoidea, 300× magnification.; **C.** *Polia* (*Metallopolia*) *kisculta* Varga, Gyulai, G. Ronkay & L. Ronkay, 2017, medial part of the antenna with long, strongly asymmetric processes, with long sensilla chaetica in terminal position, and with long, fine sensilla trichoidea, 60× magnification.; **D.** *Polia* (*Metallopolia*) *kisculta* Varga, Gyulai, G. Ronkay & L. Ronkay, 2017, stalk and dorsal processes of the antenna, with strong, slightly arcuate sensilla chaetica in terminal position, and with long and thin, nearly straight sensilla trichoidea, 120× magnification; **E.** *Polia* (*Metallopolia*) *dysgnorima* Varga, Gyulai, G. Ronkay & L. Ronkay, 2017, medial part of the antenna with long, strongly asymmetric processes, with very long, slightly arcuate sensilla chaetica in terminal position, and with long, fine sensilla trichoidea, 60× magnification.; **F.** *Polia* (*Metallopolia*) *dysgnorima* Varga, Gyulai, G. Ronkay & L. Ronkay, 2017, stalk and dorsal processes of the antenna, with strong, very long and slightly arcuate sensilla chaetica in terminal position, and with long and thin, often slightly curved sensilla trichoidea, 160× magnification.

was, however, mostly neglected. Information is mostly lacking on how the reproductive isolation is achieved between closely related species and how the antennal structures might result in some important barriers during speciation events (Xue et al. 2016).

Five basic types of sensilla were already described and characterised in first publications (sensilla trichodea, sensilla coeloconica, sensilla styloconica, sensilla chaetica, and sensilla covered by a network of grooves, see Callahan 1969; Flower and Helson 1974; Liu and Liu 1984). These types, however, have been more copiously subdivided in some recent communications (e.g. according to the length and diameter: Diongue et al. 2013, uniporous vs multiporous sensilla: Chang et al. 2015; Thammaiah et al. 2021) and variation within species was also considered (Calatayud et al. 2006; Chang et al. 2015; Thammaiah et al. 2021). Unfortunately, we could not make similar analyses due to the rather limited amount of voucher specimens in museum collections which could be truncated for our studies.

The possibilities for comparisons were also very limited for us. All surveyed species, except for *Busseola fusca* which has shortly bipectinate antennae (Calatayud et al. 2006), have ciliate male antennae only. From the Noctuidae species which have been studied up to now, only two Hadenini species, *Mamestra configurata* and *Mythimna separata*, are relatively closely related to *Ctenoceratoda*. According to the descriptions and figures (Liu and Liu 1984; Chang et al. 2015), the main types of the sensilla are essentially identical in these species. The stalk of antennae is usually densely covered by sensilla coeloconica like roofing tiles. Minor differences were discovered mainly in the more scattered versus verticil-like settling of sensilla trichoidea. However, the "flagellate" type of the sensilla trichoidea was found in both species of Hadenini. Essential similarity of the bipectinate antennae was discovered in *Busseola fusca* (Calatayud et al. 2006), in which the repartition of the scattered sensilla trichoidea and the subterminal position of sensilla chaetica on the pectinate processes proved to be very similar to the *Ctenoceratoda* species.

These morphological details of the antennal traits, however, do not allow to draw any wider taxonomic conclusions. These are actually restricted to the species groups of *Ctenoceratoda* since we only could establish some differential traits for those species groups which represent different phylogenetic lineages within the clearly monophyletic genus. The dorsal and ventral pectiniform processes are nearly symmetrical in the *C. sukharevae* group with considerable variation in length among species. These are more elongate and asymmetrical in the *C. khorgossi* and *C. tancrei* groups, while essentially shorter and asymmetrical in the taxonomically more separated *C. contempta* group. The sensilla chaetica are usually positioned terminally-subterminally on the pectiniform processes, both on the dorsal and the ventral side. These are usually strong, acute terminally, with shallow longitudinal groves. The *C. contempta* group is more differentiated in this respect as well, it is characterised by very strong, claw-shaped, curved sensilla chaetica. The sensilla trichoidea are extremely elongate and thin in the *C. khorgossi* group what seems to correlate with the length of the pectiniform processes, typical for this species group. They are more evenly dispersed in the species of this species group, while they are more arranged in verticils in the species of the *C. tancrei* and the *C. contempta* groups, and also in *C. sukharevae*. The terminally thin and „flagellate" sensilla trichoidea are present in *C. sukharevae* and in the most extreme form in the *C. contempta* group. In the *C. khorgossi* group, the very thin sensilla trichoidea are not flagellate, straight in the sister species *C. khorgossi* and *C. persephone*, but declining in *C. argyrea*.

Moreover, in some cases, we have observed malformed, fused segments (e.g. in *C. tancrei* and, most extremely, in *C. oxyptera*, Fig. 3A, B). Supposedly, these malformations can occur in species breeding in small, localised populations as possible consequences of inbreeding. Of course, the clarification of these events requires further studies.

As a next step of these surveys, the antennal structures of further genera of the subtribe Poliina will be studied, especially those of the most diverse genus *Polia*, subdivided into some subgenera and numerous species groups. While all species groups of *Ctenoceratoda* are restricted to arid and mostly to montane habitats, the *Polia* subgenera and species populate the most different temperate and cold habitats, and also show a higher variety of antennal types. It means that we can hypothesize some connections between the habitats of the species and the structures of the antennae.

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